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An emended description of the freshwater araphid genus *Ambistria*: a rare diatom from North American Eocene localities

PETER A. SIVER ⓘ*

Department of Botany, Connecticut College, New London, CT, USA

In 1968 Lohman and Andrews described the freshwater araphid diatom genus *Ambistria* from the Wagon Bed Formation, a Late Eocene deposit in Wyoming, U.S.A. The genus was distinguished from other genera on the basis of the distinctive shape of the valve coupled with short striae restricted to the valve margins, the latter resulting in a wide hyaline axial region. These authors further described two species of *Ambistria* based on differences in size and the presence/absence of randomly spaced isolated pores in the hyaline axial region. Further details could not be discerned from the specimens illustrated, and the genus has not been reported since the original description. Numerous specimens of *Ambistria* were uncovered from the Giraffe Pipe locality, an Early Eocene deposit located in the Northwest Territories, Canada, near the Arctic Circle. Examination of these specimens with light and scanning electron microscopy revealed an additional suite of characters which have now been used to emend and expand the original generic description. These features include the presence of marginal ridges, a unique mechanism used to link frustules together into chains, areolae with reniform-shaped volae, and laterally opening girdle bands. *Ambistria* belongs in the class Fragilariophyceae Round, and is best placed within the order Fragilariales (Silva) emended Round. Additional characters that could be used to delineate between species include shape of the central region, length to width ratio, and possibly the number of girdle bands. The recent discovery of *Ambistria* in the Giraffe Pipe locality extends the range of this extinct diatom to the Early Eocene.

Keywords: Ambistria, *copulae, Eocene, Fragilariales, freshwater, North America*

Introduction

Lohman & Andrews (1968) originally described the araphid freshwater diatom genus *Ambistria* Lohman & Andrews from the upper portion of the Wagon Bed Formation in Wyoming, USA. This section of the formation was determined to be Late Eocene. At the time Lohman & Andrews (1968) noted that the diatom assemblage represented by the Wagon Bed deposit was the oldest non-marine locality known in North America. Siver et al. (2018) recently reviewed the oldest known localities bearing freshwater diatoms, both in North America and worldwide. Investigations made subsequent to the Lohman & Andrews (1968) publication have uncovered additional sites bearing freshwater diatoms, including a number of older Eocene localities (e.g., Bradbury & Krebs 1995, Bullwinkel & Reigel 2001, Wolfe et al. 2006, Wolfe & Siver 2009, Siver et al. 2010, Benson & Kociolek 2012) as well as a number of much older sites from the late Upper Cretaceous (Chacón-Baca et al. 2002, Ambwani et al. 2003, Beraldi-Campesi et al. 2004, Singh et al. 2006, Siver et al. 2018). The Giraffe Pipe locality situated near the Arctic Circle in the Northwest Territories, Canada, is an especially important early Eocene site that contains an extensive number of well-preserved microfossils, of diatoms as well as chrysophytes, synurophytes, euglyphids, heliozoans and sponges (Wolfe & Siver 2009, Barber et al. 2013, Siver 2018). Currently the oldest known locality in North America harbouring freshwater diatoms is the 66.5 million year old Battle Formation, an extensive freshwater environment that stretched across much of southern Alberta and into southwestern Saskatchewan, Canada, during the late Upper Cretaceous (Siver et al. 2018).

A total of 34 diatom species were uncovered from the Wagon Bed Formation including 27 described as new, indicating that the site was quite distinct from later (younger) assemblages known at the time from North America (Lohman & Andrews 1968). The formation was especially rich in species of *Pinnularia* Ehrenberg, *Fragilaria* Lyngbye and *Aulacoseira (Melosira)* Thwaites, with 12, five and six species from each genus respectively. Among the newly described taxa were two species of the proposed genus *Ambistria*. *Ambistria* has not been reported since the Lohman & Andrews' (1968) study. Despite multiple efforts original material from the Lohman & Andrews (1968) work has not been located to use for further study.

*Corresponding author. E-mail: pasiv@conncoll.edu

lac]Recently, an extensive number of *Ambistria* specimens which clearly match the original description, were uncovered from the Giraffe Pipe locality and examined with light and scanning electron microscopy (SEM). This resulted in a fuller and more detailed analysis of the genus. The purpose of this contribution is to present an emended description for *Ambistria* and compare it with other araphid genera in the Fragilariophyceae.

Materials and methods

Site and core description

Detailed descriptions of the Giraffe Pipe locality are given in Siver et al. (2015) and Wolfe et al. (2017). Briefly, the Giraffe Pipe fossil locality (64° 44^t N, 109° 45^t W) is situated within a crater formed during emplacement of a kimberlite diatreme into the Slave Craton, Northwest Territories, Canada, approximately 47.8 million years ago during the early to middle Eocene (Siver & Wolfe 2005; Wolfe et al. 2006). This places the origin of the site at the boundary between the Ypresian (56–47.8 Ma) and Lutetian (47.8–41.2 Ma). The crater harboured an aquatic environment that remained for thousands of years then transitioned to a terrestrial environment. The aquatic and terrestrial sediments were subsequently capped by Neogene glacial deposits (Siver & Wolfe 2005; Wolfe et al. 2006). The Giraffe Pipe is one of many kimberlites emplaced in the Lac de Gras region between the Late Cretaceous and middle Eocene (Heaman et al. 2004).

A 163 m long core, drilled at a 47° angle, was recovered from the Giraffe maar in 1999 by BHP Billiton Inc. (Siver & Wolfe 2009). The lower 113.1 m of the core contains well-preserved, stratified organic sediment, including 68.3 m of lacustrine mudstone deposited during early phases of the Lutetian. The remains of the core are stored in wooden boxes. Each core box has three 1.5 m long channels, holding a total of 4.5 m of material. Samples from the core are identified with a three part number (Siver 2015). The first number represents the core box. The larger the number, the deeper the section is within the core. Seventeen boxes, numbers 27 through 11, contain lacustrine sediments, with box 11 representing the end of the aquatic environment. The second number represents the channel within the box. The third number is the measurement in cm from the top of a core length. For example, sample 19-1-100 represents the sample taken from 100 cm down along the core length positioned in channel 1 from box 19.

Laboratory methods

This study includes two samples taken from 19-1-100. Mudstone fragments (0.5–1.0 g) were oxidized using 30% H_2O_2 under low heat for a minimum of 1–3 h, rinsed with distilled water, and the slurries stored in glass vials at 4° C. This mild oxidation procedure was enough to
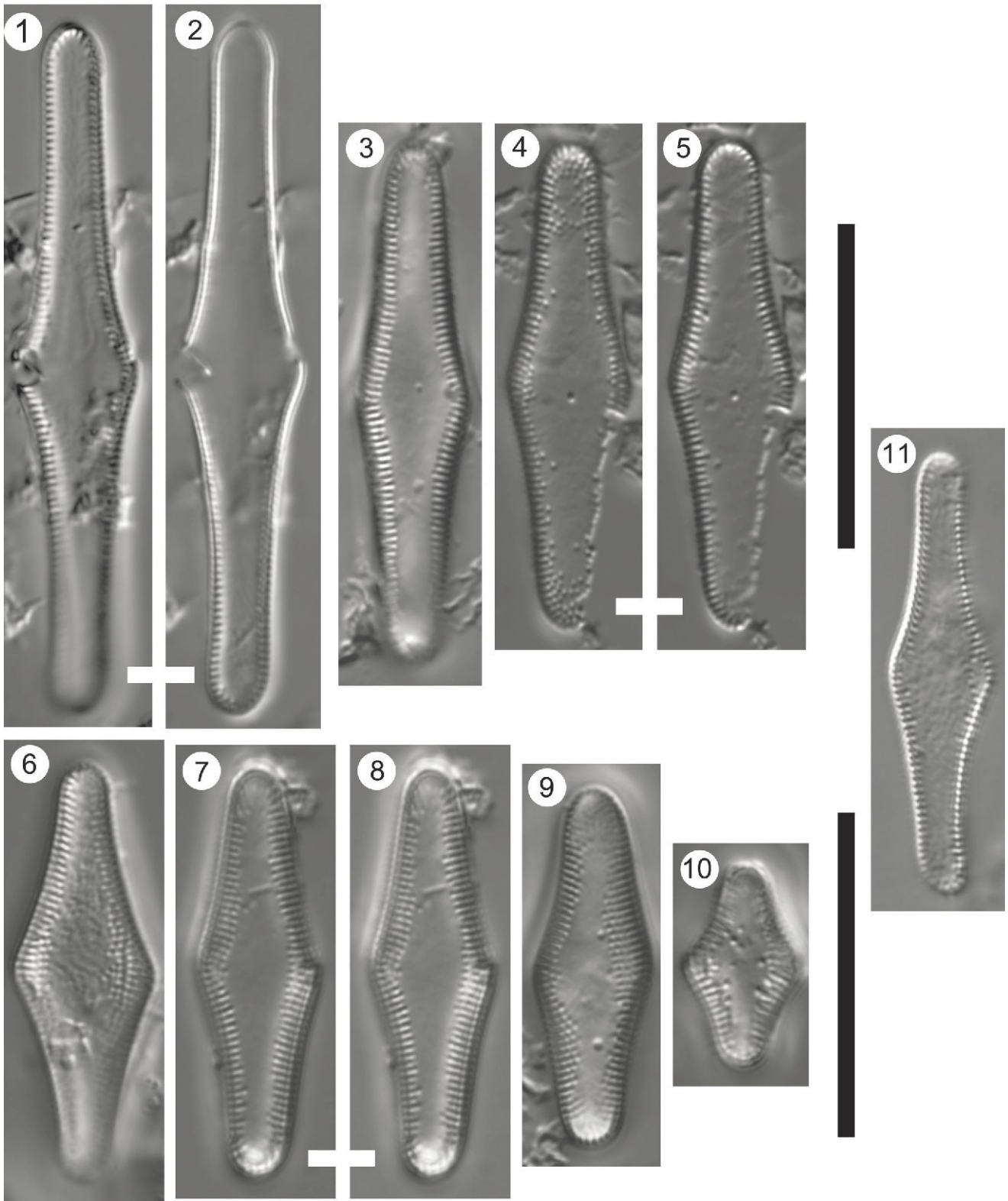
separate numerous microfossils from the mudstone matrix. An aliquot of the resulting slurry was air dried onto a piece of heavy duty aluminium foil, trimmed, and attached to an aluminium SEM stub with Apiezon wax. Samples were coated with a mixture of gold and palladium for 2 min with a Polaron Model E sputter coater, and examined with an FEI Nova NanoSEM 450 FESEM. Aliquots were also dried onto coverslips, mounted onto glass slides using Naphrax, and examined with a Leica DMR light microscope with a Zeiss Axiocam 503 colour camera. Morphometric data were made directly from SEM images. Additional length and width measurements were made with light microscopy using Zeiss camera software.

Results

Numerous specimens of *Ambistria* were uncovered in stratum 19-1-100 of the Giraffe Pipe core. Specimens were extracted relatively easily from the core rock with hydrogen peroxide treatment. However, despite the mode of preparation most frustules remained intact, often in short chains, and therefore came to rest on the glass coverslips or SEM preparations in girdle view. In addition, most isolated valves were still connected to several copulae, which resulted in these specimens coming to rest with the valve face on the SEM stub. As a result, valve face views were more difficult to find, especially on the SEM stubs, whereas numerous specimens were studied in girdle view. Despite this difficulty, over 40 specimens were examined in valve view.

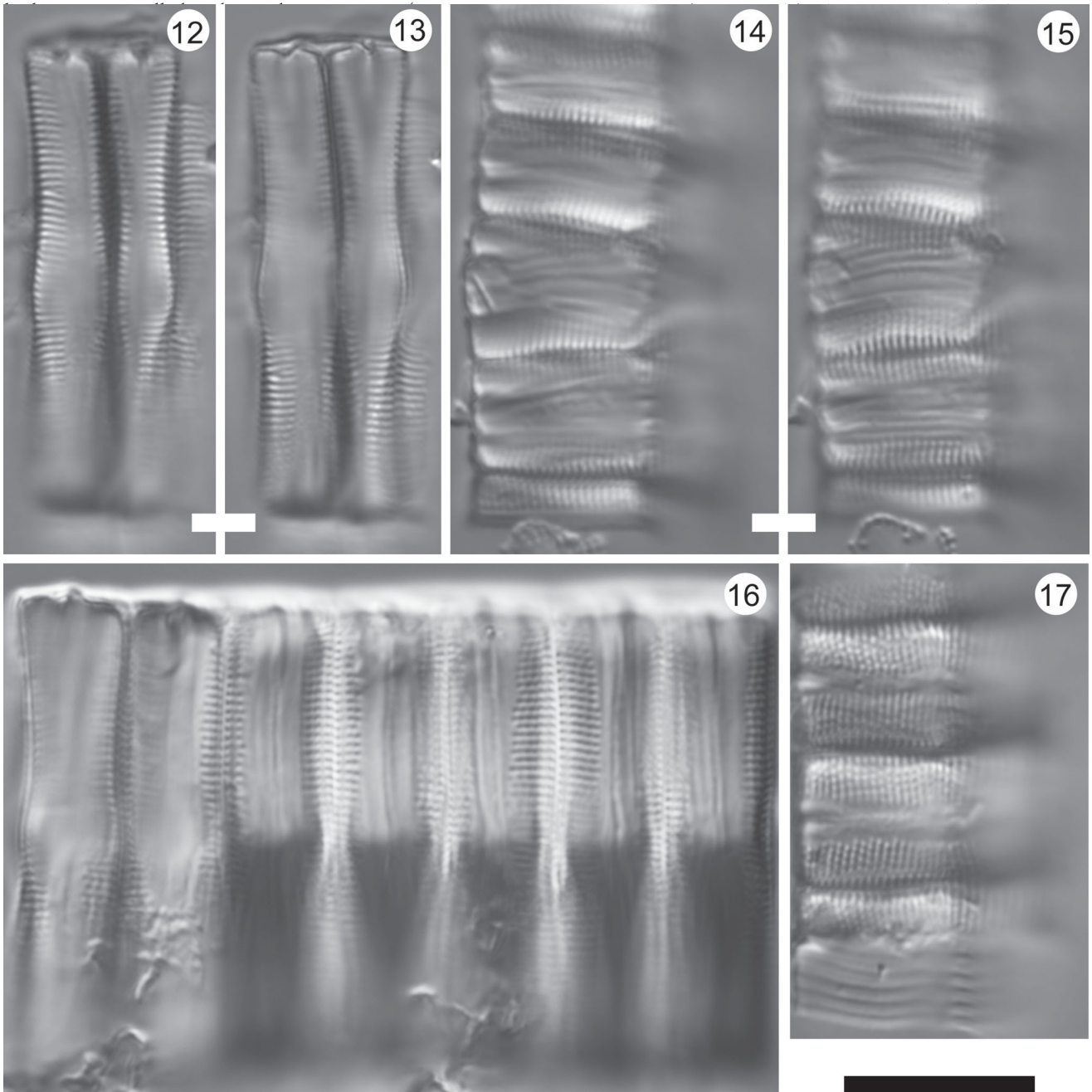### *Ambistria* Lohman & Andrews (Figs 1–36)

Emended description: Frustules attach to form filaments. Valves are linear, elongate, with a central widening, and broadly rounded apices (Figs 1–10, 18–24). The valve margin between the apex and centre ranges from straight (e.g. Figs 21–22) to concave (e.g. Figs 19–20), the latter shape resulting in more pronounced central widening. Valve face striae are uniseriate, short, restricted to the margin, and usually consist of 2–4 areolae (Figs 1–10, 18–21). Striae are subparallel or slightly divergent, continue uninterrupted around the apices, and range from 22–24 per 10 μm on most specimens, rarely up to 26 per 10 μm. The axial region is broad, completely hyaline (Figs 7–8, 11, 18) or with scattered areolae in addition to those in the marginal striae (Figs 9–10). The mantle is relatively deep, especially on smaller valves, forming a right angle with the valve face, striated, and terminates in a hyaline collum that often has a row of irregularly shaped plaques (Figs 18, 34, 36). A step is often observed on the mantle close to the collum (Figs 18, 36). The mantle striae are continuous with those on the valve face, but longer (Figs 18, 25) and composed of 4–7 areolae. The most marginal areolae of the valve face striae, and the mantle areolae closest to the valve face margin, are usually larger in diameter than the remaining areolae (Figs 27, 33). Areolae range

Figs 1-11. Light micrographs of *Ambistria* depicting the range of valve shapes fonnd at the Giraffe Pipe locality. Scale bar = 20)l!ll.

in shape from circular to oval, to very elongated, and are covered externally with volae (Figs 29-34). Smaller areolae tend to have a single reniform-shaped vola, but the number of outgrowths is variable and two or more flap-like outgrowths per areola are common (Figs 29-30). The areolae on the mantle bordering the marginal ridge can be
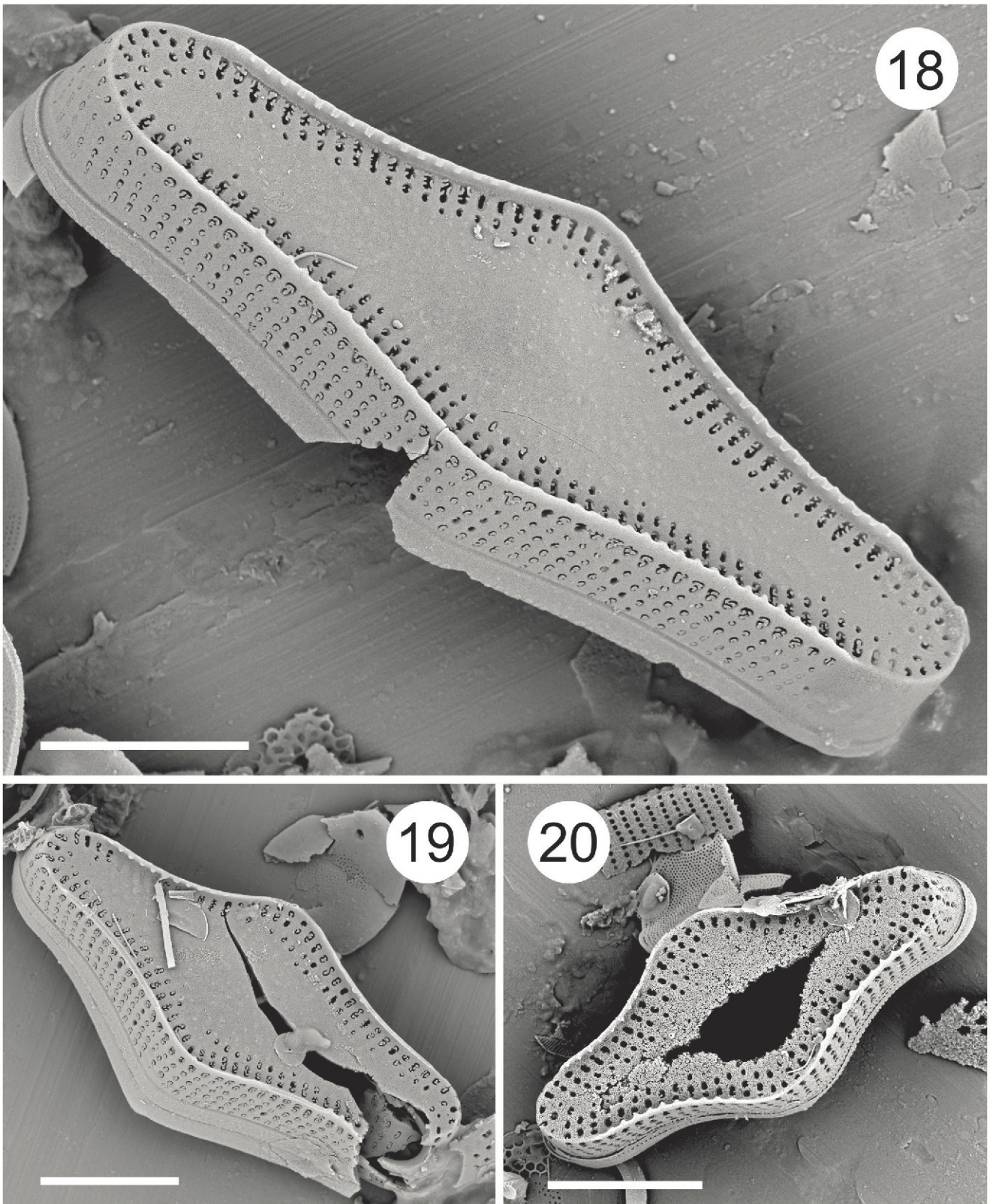
Figs 12–17. Light micrographs of filaments of *Ambistria* in girdle view found at the Giraffe Pipe locality. Note the swollen central area, long mantle striae and range in the number of girdle bands. Scale bar = 10 μm.

highly contorted, and are sometimes fused together within or between striae to form very elongate openings (Figs 29–30, 36). Internally, the areolae within a stria are covered with a continuous, thin layer of silica that is flush with the inner valve surface (Figs 21–23, 26). Valves lack rimoportulae and apical pore fields.
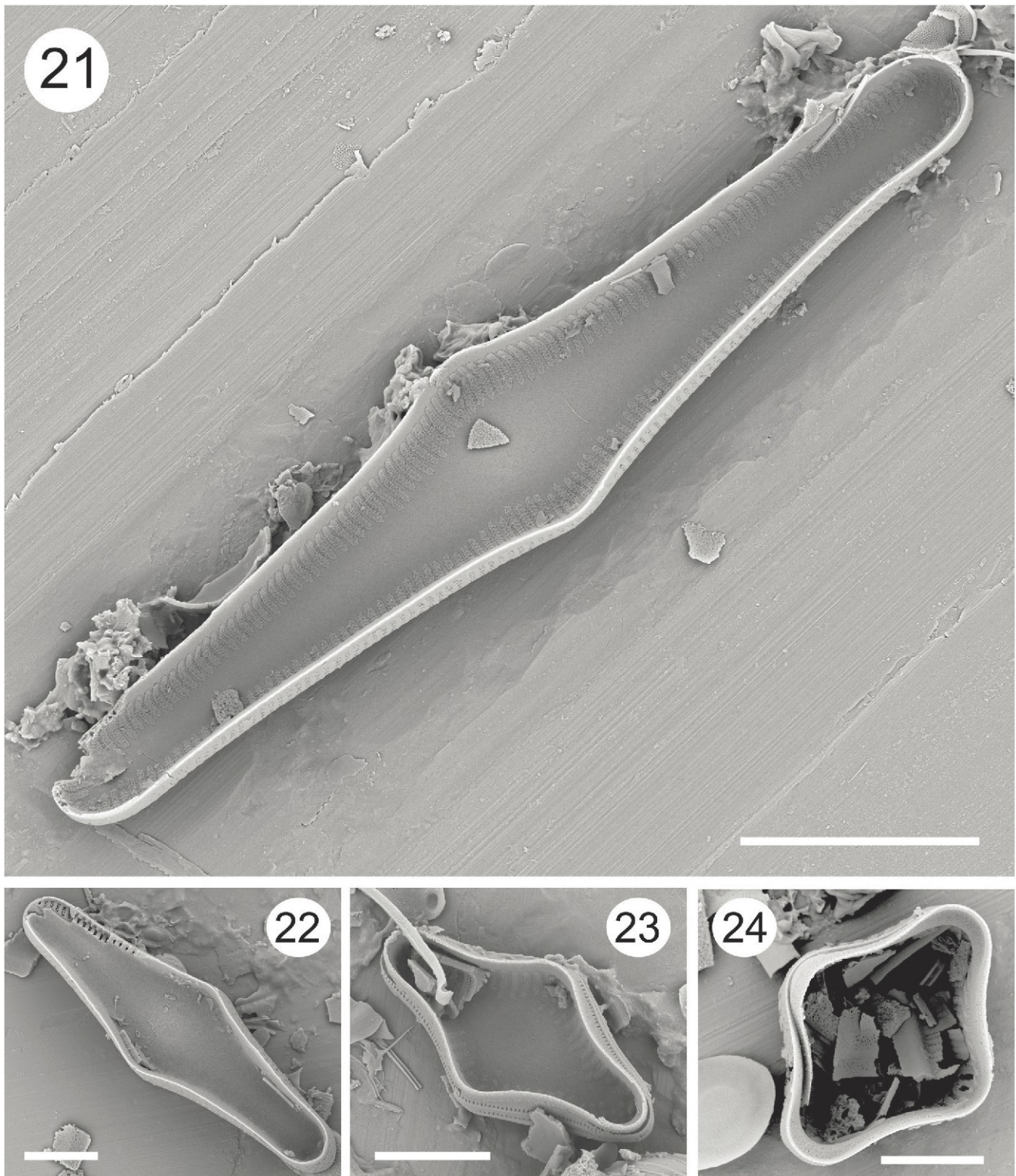
A siliceous ridge extends vertically from the valve face margin, but does not extend around the apices (Figs 18–20, 29–33). A series of small, blunt projections, evenly spaced with the striae, line the inner side of the marginal ridge

(e.g. Figs 25, 27–28). The projections attach to areolae on adjoining valves (Fig. 28); this serves as a means of linking frustules to form chains. Given this connecting mechanism only one valve per frustule has a marginal ridge, and the valves at the ends of chains typically lack such a structure (e.g. Fig. 34).

The number of girdle bands (copulae) forming the cingulum ranges from a few to numerous (Figs 12–17, 31–36). It is not uncommon for the cingulum to consist of between 10–15 girdle bands per frustule (e.g., Figs 14–15, 31–36),
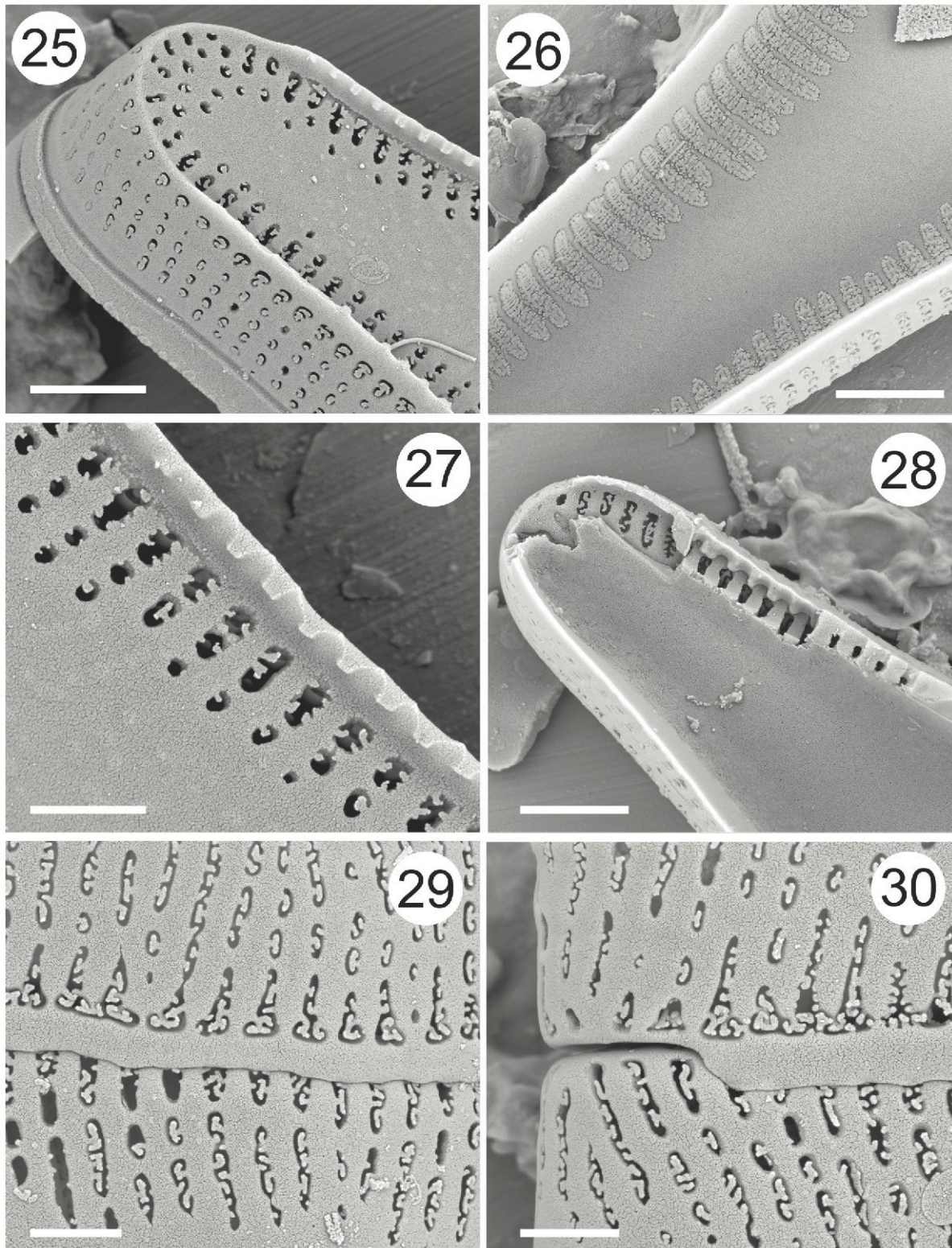
Figs 18-20. SEM micrographs of *Ambistria* valves showing the widened central area and broadly rounded apices, and highlighting the valve face. Note the short marginal striae, marginal ridges, wide and hyaline axial region, and the nature of the mantle. Scale bars = 5 lliil·
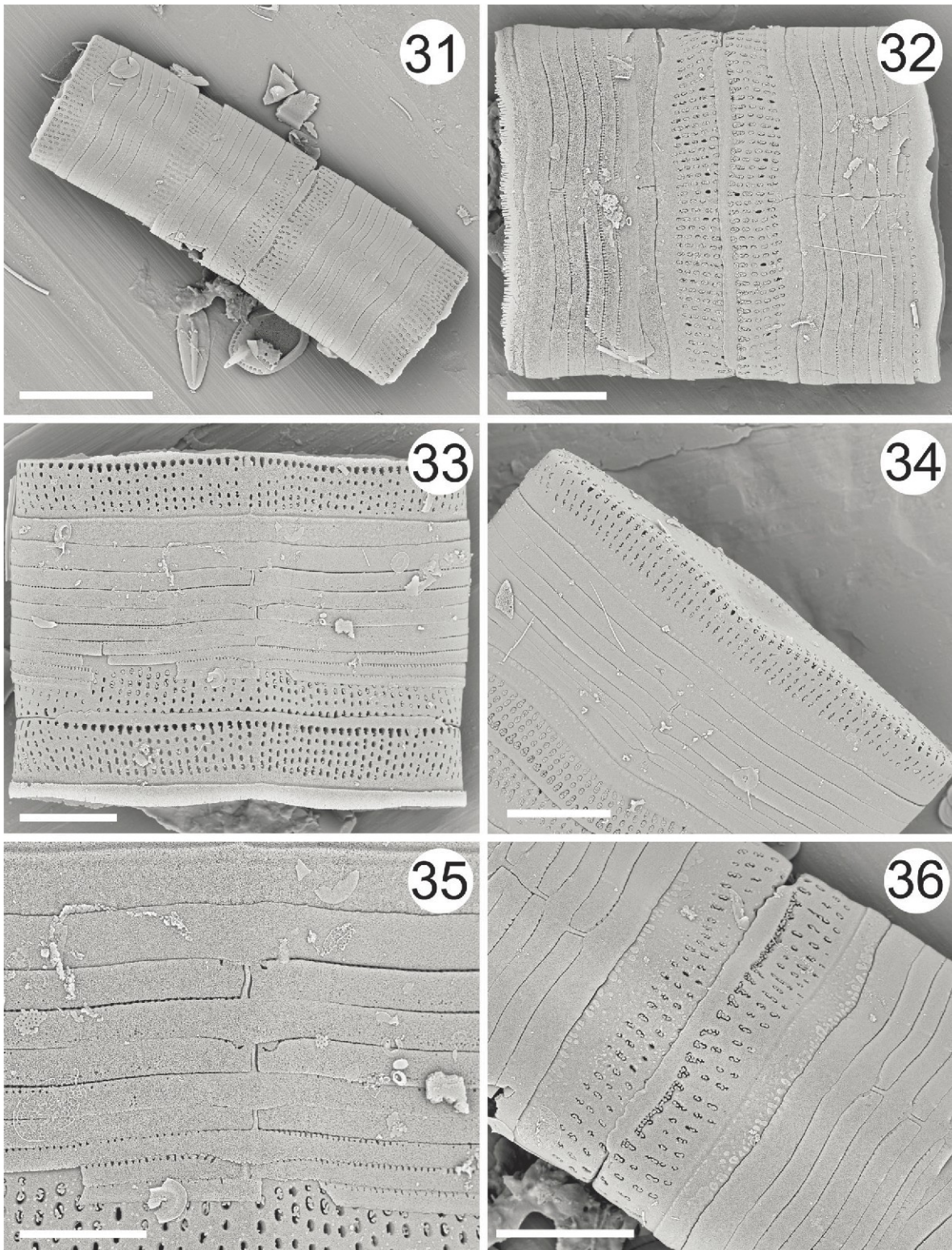
Figs **21-24.**   SEM micrographs of *Ambistria* valves showing the internal valve surface, and depicting a range of valve shapes. Fig. 21. Elongated valve with a smaller central widening and a correspondingly large length to width ratio. Fig. 22. Valve type depicting the most common shape. Figs 23-24. Smaller valves each with an extended central widening and a small length to width ratio. Scale bars= 10)ⅼiⅼ (Fig. 21), 5)ⅼiⅼ(Figs 22-23) and 3)ⅼiⅼ(Fig. 24).

and up to 17 have been observed. Longer frustules tend to have fewer copulae, with the larger numbers being found on smaller frustules. The margin of the valvocopula where it attaches to the valve is lined with fimbriae. Girdle bands open laterally at the centre of the valve (Figs 33--35). Each girdle band has a long, thin ligule, and a single row

Figs 25-30. SEM micrographs of *Ambistria* valves. Fig. 25. Close-up of the apical end of the valve showing the continuous nature of the striae around the apex, areolae with various-shaped volae, the marginal ridge with short projecting teeth, and a few isolated punctae on the wide axial region. Fig. 26. Close-up of the internal side of a valve showing the continuous siliceous sheet covering the areolae within each striae. Fig. 27. Close-up of the teeth on the marginal ridge. Note the alignment with the striae. Fig. 28. Connection of two adjoining valves. Note the projections along the marginal ridge of the bottom valve connecting to the areolae of the top valve. Figs 29-30. Close-ups of the mantle in girdle view depicting connection of adjoining valves. Note the position of the marginal ridge and the highly variable-shaped areolae and corresponding volae. Scale bars = 2㎛ (Figs 25, 26, 28) and 1㎛ (Figs 27, 29, 30).

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Figs 31-36.   SEM micrographs *ofAmbistria* frustules in girdle view. Fig. 31. Three frustules in a filament each with munerous copulae. Note the wide striated mantle, the laterally opened nature of the girdle bands and associated ligules, and the marginal ridges. Fig. 32. Valves of two connecting frustules, both with numerous girdle bands. Note the fimbriae of the valvocopula on the left valve. The valve that it attaches to has fallen off. Fig. 33. Three valves depicting the wide striated mantle, marginal ridge connecting the lower two valves, and copulae. Note the single row of closely spaced and elongated pores on the advalvar edge of the girdle bands, especially on the bands that are broken. Fig. 34. Frustule on the end of a filament showing numerous girdle bands, a wide mantle, and the marginal striae and hyaline axial region on the valve face. Note the lack of a marginal ridge on this terminal valve. Fig. 35. Close-up of the cingulum on the specimen in (Fig. 33). Note the narrow ligules. Fig. 36. Connecting frustules within a filament showing the extent of the marginal ridge, and the fact that this structure does not continue around the apices. Note the fused areolae on the mantle aligning the marginal ridge on the lower valve, and the collum with a row of plaques. Scale bars = 10 **lllil** (Fig. 31), 5!lm (Figs 32-34), 4 **lllil** (Fig. 36), and 3lllll (Fig. 35).

of closely spaced and elongated pores are present on the advalvar edge (Fig. 35).

Museum Specimens: Two permanent glass slide preparations of material from section GP 19-1-100 of the Giraffe Pipe core with ample specimens of *Ambistria* have been deposited at the Canadian Museum of Nature (CANA 128453). These are the same slides that contain numerous specimens of the cyst produced by *Mallomonas ampla* (Siver & Lott 2012).

Morphometrics: Morphometric measurements were made on 40 specimens. Length and number of striae per 10 μm were estimated for each specimen, and width for 15 specimens imaged in valve view. The length ranged from 8.8–48 μm, with mean and median values of 22 and 21 respectively. Except for two specimens, valve lengths of the remaining specimens were < 31 μm. Valve width ranged from 6.3–9.5 μm, with mean and median values of 7.3 and 7.1 respectively. The relationship between valve width (measured at the central swollen region) and length (independent variable) was modestly significant ($p = 0.008$, $r^2 = 0.41$) and indicates that as valve length decreases, so does valve width. Although the number of striae per 10 μm ranged from 20–25 on Giraffe specimens, the value for 35 specimens ranged from 22–24.

Coexisting organisms: The 19-1-100 stratum from the Giraffe Pipe core contains an extensive diversity of siliceous organisms, including other diatoms, chrysophytes, synurophytes, heliozoans, euglyphid plates and sponge spicules. The stratum is dominated by *Aulacoseira giraffensis* Siver, Wolfe & Edlund and numerous scales representing multiple species of *Mallomonas* Perty and *Synura* Ehrenberg. Like *Ambistria*, specimens of *Fragilariforma virescens* (Ralfs) Williams & Round and *Nupela mutabilis* Siver, Wolfe & Edlund were also common in this section of the core. Remains of the synurophyte *Mallomonas ampla* Siver & Lott were equally abundant as *A. giraffensis*. Remains of *Mallomonas insignis* Penard, *M. asmundiae* (Wujek & Van der Veer) Nicholls and *Synura recurvata* Siver & Wolfe were also common, and the stratum contains a wide diversity of chrysophyte cysts. Scales of the chrysophyte genera *Paraphysomonas* and *Clathromonas* were abundant, and samples also contained scales of multiple heliozoan species, plates of both *Scutiglypha* and *Euglypha*, and sponge spicules.

Discussion

According to Lohman & Andrews (1968), the distinctive shape of the valve, coupled with the short marginal striae, are the two characters that best distinguish *Ambistria* from other araphid genera. Given the findings in this study, the distinguishing characters can be expanded to include the marginal ridges on the valve, the unique mechanism that links together frustules to form chains,

areolae with reniform-shaped volae and laterally opening girdle bands. The marginal ridge on *Ambistria* valves is unique among genera in the Fragilariophyceae. Many araphid genera possess a row of marginal spines, but not a continuous siliceous structure as produced by *Ambistria*. Genera that possess marginal spines have them on both valves and spines interlink to hold cells together in the filament. *Ambistria* frustules are heterovalvar, only one valve possesses the ridge and uses projections to attach to the ridgeless valve on the adjoining frustule. This method of attachment, coupled with the heterovalvar nature of the frustules, is unique among araphid diatoms. A few species of *Oxyneis* also form a marginal ridge (Siver & Hamilton 2011), but this structure consists of a series of fused spines of variable lengths and is morphologically different from the continuous ridge found on *Ambistria*.

Although some diatom genera, such as the raphid genus *Gomphonema* Ehrenberg, have areolae with similar reniform volae, this type of velum is not found in other araphid genera. Like *Ambistria*, many araphid genera possess open copulae with ligules and a single row of pores on the advalvar side. However, the girdle bands on *Ambistria* specimens open laterally, whereas in other genera within the Fragilariophyceae they open apically (Round et al. 1990, Siver & Hamilton 2011). Lastly, *Ambistria* valves lack rimoportulae. Collectively, this expanded suite of features, especially the heterovalvar nature of the frustule and copulae that open laterally, clearly distinguishes *Ambistria* from all other araphid diatom genera.

One other genus is worth mention in comparison to *Ambistria*. *Rimoneis* M. Garcia is a recently described genus from freshwater to brackish habitats in Brazil (Garcia 2010) that shares some features with *Ambistria*. Like *Ambistria*, *Rimoneis* is a hyaline araphid diatom with short marginal striae that continue down the mantle, and with frustules that link together into filaments. The type species *R. inanis* M. Garcia also possesses marginal ridges, and both genera lack rimoportulae (Garcia 2010). However, the marginal ridge structure, areola coverings and valve shapes are very different between the two taxa. The marginal ridges on *Rimoneis* valves have a central linear canal and lack the connecting mechanism found on *Ambistria*. In addition, the laterally opening girdle bands on *Ambistria* are unique, and *Ambistria* lacks apical pore fields. Despite some similarities, these two genera are very different.

The suite of characters for *Ambistria* supports placement of this genus in the Fragilariales, and not Tabellariales Round. This is based on the structure of the copulae and the absence of a rimoportula. Although the large number of girdle bands produced by *Ambistria* cells is similar to those formed by genera in the Tabellariales (e.g., *Tabellaria* Ehrenberg and *Oxyneis* Round), those of *Ambistria* lack septae. In addition, valves of species in the Tabellariales including *Tabellaria* and *Oxyneis* have a rimoportula. In contrast, taxa in the Fragilariales

lack sentate girdle bands, and genera may (e.g., *Fragilaria* Williams & Round and *Fragilariforma* Williams & Round) or may not (e.g., *Staurosira* (Ehrenberg) Williams & Round, *Pseudostaurosira* (Grunow) Williams & Round and *Pseudostaurosiropsis* Morales) have rimoportulae (Round et al. 1990). In conclusion, as currently defined *Ambistria* is best placed in the Fragilariales. However, it is noted that given the wide range of stria and areola structures found within genera comprising the Fragilariales, coupled with the presence/absence of rimoportulae and apical pore fields, reorganization of the order may be warranted.

When Lohman & Andrews (1968) originally described *Ambistria* they proposed two species, *A. hyalina* Lohman & Andrews and *A. punctata* Lohman & Andrews. *Ambistria hyalina* was distinguished from *A. punctata* by virtue of its longer valves and, more importantly, the fact that it lacked randomly scattered puncta in the hyaline axial region. Lohman & Andrews (1968) further noted that they could not distinguish between the two species in girdle view. The hyaline axial region lacking additional puncta on *A. hyalina* is clearly observed in each of the three specimens illustrated by Lohman & Andrews (1968; Figs 21, 29 and 30), as are the three specimens of *A. punctata* with scattered pores (1968; Figs 26, 28 and 31). In the current study, many of the valves could be separated into two groups as Lohman & Andrews (1968) did on the basis of the presence/absence of scattered puncta within the hyaline region. Additional characters can be assigned to these two groups. First, the margins of the *A. punctata* group (e.g., Figs 6, 10) tend to be more gradually concave and less straight than in *A. hyalina* specimens (e.g. Figs 1, 3, 21) yielding a central widened region that extends further along the length of the valve. Second, the length to width (at valve centre) ratio is smaller for *A. punctata* specimens often close to or less than 2.5. On the other hand, the length to width ratio for many *A. hyalina* specimens is 3–6. Third, the mantle is deeper with longer striae on valves of *A. punctata*. Lastly, although more difficult to determine, frustules matching *A. punctata* appear to produce more girdle bands than specimens of *A. hyalina*.

It was not always straightforward to separate specimens into *A. hyalina* or *A. punctata* using the criteria given by Lohman & Andrews (1968) and it is possible that additional taxa are also present. The range in length of Giraffe specimens (9–48 μm) best fits the range given for *A. punctata* (16–45 μm) and longer valves reported for *A. hyalina* (up to 85 μm) were not found. On the other hand, the range in valve width of the Giraffe specimens was a closer match to *A. hyalina*. On some valves (e.g. Fig. 18) additional puncta possibly associated with the striae, were observed near one or both apices, but additional puncta were lacking on the remaining portion of the axial region. Perhaps these specimens represent a third closely related taxon. On other specimens, the terminal areolae of the valve face

striae were often spaced further out onto the hyaline area yielding yet another morph. It is further possible that all the morphs observed represent one species, and that as the length of the valve decreases there is a tendency to produce the random areolae and additional girdle bands. Distinguishing between the species is further complicated since the genus has only been observed at two sites, and in both cases a mix of specimens was uncovered. If indeed these two taxa are separate species, it stands that eventually, populations of one will be uncovered independent of the other. Given the rarity in which this genus has been observed, additional populations should be examined before making further species determinations.

With few exceptions, it is well known that the mean valve size of a diatom population decreases with continued cell division (Round et al. 1990). For many pennate diatoms, the overall shape of the valve often changes with size reduction, and the length usually decreases more than the width with each division. Although the width of *Ambistria* valves declined with reduction in length, the slope (coefficient) of this relationship is small (0.05), indicating a very slight change in width relative to length as frustules decrease in size. Also, the central swollen region remains prominent with size reduction. Perhaps the laterally opening girdle bands are more flexible in the middle of the valve and better enable *Ambistria* cells to maintain the shape of the centre of the valve as cell length declines.

Ambistria is now definitively known from the Early Eocene (this paper) to the Late Eocene (Lohman & Andrews 1968). Siver et al. (2018) noted that fossil remains from the Battle Formation may also contain *Ambistria*. Although the Battle Formation specimens were poorly preserved, making the identification tentative, they did display a diatom with short marginal striae, longer striae on the mantle and a valve shape consistent with *Ambistria*. Assuming a presence in the Battle Formation, *Ambistria* would be known from three North American fossil localities spanning approximately 25 million years. Interestingly, *Ambistria* has not been uncovered in the many previously studied Neogene deposits from North America (e.g., Krebs et al. 1987, Bradbury 1988), supporting the hypothesis that this genus went extinct sometime between the end of the Eocene and the Miocene.

According to Lohman & Andrews (1968) *Ambistria* grew in a shallow freshwater habitat in a warm-temperate to subtropical climate. The site supported palm trees further indicating that winter temperatures were above freezing and ice-free (Greenwood & Wing 1995). These climatic conditions are similar to those reconstructed for the region harbouring the Giraffe Pipe waterbody, where Wolfe et al. (2017) reported significantly wetter conditions, a mean annual temperature 17° C warmer than today and winter temperatures above freezing. In addition, warm

water synurophytes, diatoms, sponges and palm remains have been uncovered from the Giraffe core (Siver & Wolfe 2009, Pisera et al. 2013). A large number of palm phytoliths has also been uncovered in the lacustrine remains from the Battle Formation, also indicating a warm climate lacking winter freezing conditions. In summary, available data indicate that *Ambistria* may be an indicator of historically warm climates.

ORCID

Peter A. Siver   http://orcid.org/0000-0001-5956-8889

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